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Effects of uncertainty and target displacement on the latency of express saccades in man

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Abstract

Saccadic eye movements generated in response to a gap paradigm in which the fixation light spot was extinguished 200 ms prior to presentation of the target light spot showed appreciably shorter latencies than for the overlap paradigm in which the target light spot was presented 200 ms prior to extinction of the fixation light spot. When there was unpredictability in the direction of target presentation, i.e., to the left or right of the fixation light spot, the gap paradigm evoked mainly fast regular saccades of peak latency of 155 ms with relatively few express saccades which were defined as having latencies of less than 120 ms. By contrast, when the target always appeared to the right, a substantial population of express saccades with peak latency 95 ms was now generated. There was also a change in the relationship between saccadic latency and target angular displacement which covered the range 5–35 °. With the overlap paradigm and unpredictability of target direction, the latencies of the slow regular saccades increased markedly with target angular displacement. This was not the case with the same target direction when the latency of slow regular, fast regular, and express saccades remained constant with increasing target angular displacement. This indicates for targets appearing in the same hemifield that the ocular motor system operates with shortest latency irrespective of target angular displacement.

Keywords: Saccades; Express saccades; Overlap paradigm; Gap paradigm; Uncertainty

1. Introduction

Saccades are the rapid eye movements which rotate the eyes to bring a peripheral image of interest onto the fovea where it is held under fixation. The afferent pathway is extended and involves the primary visual cortex (Schiller, Stryker, Cynader, & Berman, 1974) and prestriate area V2 (area 18) (Abel, O'Brien, Lia, & Olavarria, 1997) which project to the superior colliculus where visual cells and quasi-visual cells drive the output neurones, the saccade-related neurones (Mays & Sparks, 1980). Saccades are also driven from the frontal eye fields (area 8) (Bruce & Goldberg, 1986) and parietal cortex (area 7) (Lynch, Mountcastle, Talbot, & Yin, 1977). The output pathway consists of projections to the paramedian pontine reticular formation and extra-ocular motor nuclei (Fuchs, Kaneko, & Scudder, 1985). Consequently saccade generation occurs only after a considerable latency period. Previously, we were prompted to investigate the dependence of the saccadic latency on target angular displacement (Darrien, Herd, Starling, Rosenberg, & Morrison, 2001) by what seemed to be a discrepancy between reports of substantial increases in saccadic latency (e.g., Fuller, 1996) and the faster axonal conduction velocity of more peripheral retinal ganglion cells (Ogden & Miller, 1966). The outcome of our study was that, for changes in target angular displacement and in the direction of gaze, saccadic latency remained constant. It was not possible to conclude that the ocular motor system was operating at maximal performance regardless of target location since there is a category of saccades of shorter latency than those which we recorded. When, as in our study, the fixation light spot is present when the target light

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spot appears (overlap paradigm), saccadic latencies peak at around 220 ms. However, when the fixation light is extinguished prior to target appearance (gap paradigm), the saccadic latency shortens appreciably (Saslow, 1967). Even shorter latency saccades, known as express saccades, may also be generated with the gap paradigm (Fischer & Ramsperger, 1984) so that three categories of saccades can be identified according to their latency distribution: slow regular saccades evoked by the overlap paradigm have latencies of 200–220 ms while the gap paradigm evokes fast regular saccades with latencies of 135–170 ms and express saccades with latencies of 70–120 ms (Gezeck, Fischer, & Timmer, 1997). Express saccade generation has been linked to the disengagement of fixation neurones in the foveal representation of the superior colliculus caused by removal of the fixation light (Dorris & Munoz, 1995; Sommer, 1994). More recently, the increased excitability of saccade-related neurones following the disengagement of fixation has been proposed to generate express saccades (Dorris, Paré, & Munoz, 1997; Sommer, 1997) which was confirmed by Sparks, Rohrer, and Zhang (2000) who also established that express saccades and regular saccades are driven by the same saccade-related neurones. These data obtained from primate appear to be transferable to human in that activation of the superior colliculus has been shown by functional magnetic resonance imaging to occur on disengagement of a central fixation target (Neggers, Raemaekers, Lampmann, Postma, & Ramsey, 2005).

The issue we have thus, set out to explore was whether express saccades show the same invariance in latency with target angular displacement as slow regular saccades generated in response to the overlap paradigm. If this proved to be the case, one could then conclude that the saccade generation system operates at the shortest latency irrespective of target angular displacement.

2. Methods

2.1. Subjects

Saccadic recordings were undertaken in four naive subjects (two males and two females), ages 20–21 year, who had a Snellen acuity of 6/4, normal binocular single vision, normal amplitude of accommodation of ca. 10 DA and heterophoria determined with the Maddox rod test of no more than 2 Δ at 6 m. One subject required a spectacle correction of −1.50 DS in the right eye and −2.25 DS in the left eye. All subjects were right handed. The experiments were undertaken with the approval of the Faculty Ethics Committee of the University of Glasgow.

2.2. Recording apparatus

Saccadic eye movements were recorded by electro-oculography as described previously (Darrien et al., 2001). While this method has limitations, particularly with respect to the determination of saccadic velocity, it has its place in the determination of binocular saccadic latencies in response to large angular subtenses (Becker, 1989). The recording electrodes were silver cup electrodes and were placed as follows: the active electrode on the right temple, the indifferent on the left temple, and the earth on the forehead. The electrodes were connected to a differential preamplifier of gain 100× and bandwidth DC-100 Hz and standing potentials were annulled with a variable DC offset control. The preamplifier output was passed through a further amplification stage of 10×, which incorporated a 50 Hz notch filter. The output was recorded and analyzed with a computer-based data acquisition system which sampled at a rate of 2 kHz.

2.3. Stimulus display

This took the form of two Tektronix 502 oscilloscopes (P2 phosphor, peak emission 540 nm) from which the graticule had been removed and which had had their time bases turned off to produce stationary light spots. The oscilloscopes were positioned on their sides and top-to-bottom with their screens co-planar in the subject's frontal plane at 28.5 cm from the subject. The right beam of the left oscilloscope (in reality the upper beam) and the left beam of the right oscilloscope (lower beam) were used as fixation light spots while the two companion beams were used as target light spots. Each fixation light spot was aligned to its own chin rest which allowed the subject to view it directly without assuming an eccentric direction of gaze. The time of appearance of each beam was controlled by a Digitimer which also provided the external trigger for the computerized data collection. The beams which had an angular subtense 0.6 min arc were set to the same maximum intensity at which there was an absence of a halo: this was determined by attenuation of the beam with neutral density filters until the beam was just visible to be 4.7 logarithmic units above the photopic threshold. The subject was instructed to direct his/her gaze towards the relevant fixation light spot (the other fixation light spot being absent) and then to execute a saccade to the target light spot which appeared to the left or right in random sequence.

2.4. Experimental protocols

Two paradigms were employed viz. an overlap paradigm in which the fixation light spot appeared from 0.000 to 3.200 s and the target appeared from 3.000 to 4.500 s, and a gap paradigm in which the fixation light spot appeared from 0.000 to 3.000 s and the target appeared from 3.200 to 4.500 s. The cycle period was varied continually between 5 and 8 s. Each experimental run involved the recording of 12 or 24 saccades at each of eight target angular displacements extending from 5° to 35° presented in random sequence for both overlap and gap paradigms. No feedback was given to the subjects due to its alleged effect of inducing express saccades (Kingstone & Klein, 1993). In Experiment 1, the groups of 24 saccades were evoked by target light spots which appeared to the left or right of the fixation light spot in random sequence. Two complete experimental runs were undertaken. In Experiment 2, groups of 12 saccades were recorded in which the target light spot always appeared to the right and three complete experimental runs were undertaken. Control experiments were also undertaken to test whether the adoption of a viewing distance of 28.5 cm might have affected saccadic latencies due to unusual proprioceptive feedback or efference copy arising from the amount of convergence exerted (Donaldson, 2000). Saccadic latencies for natural viewing at 57 cm were compared to those obtained when viewing through a 10 Δ prism placed base-out to induce adduction and simulate viewing at 30 cm and base-in to induce abduction to simulate viewing at 400 cm. In these experiments, the overlap paradigm and target presentation to the right were used.

2.5. Data analysis

Prior to the main recording sessions, a calibration procedure was undertaken to confirm the linearity of measured saccadic amplitude against stepwise displacement of the eyes in leftwards and rightwards directions over a range of up to 35°. Then, from the main body of results, the latency was taken as the time from the appearance of the target to the start of the saccadic eye movement which was indicated by the small notch resulting from the synchronized depolarization of the extra-ocular muscles (Thickbroom & Mastaglia, 1985). The relationship between latency and target angular displacement was tested by linear regression analysis using the Minitab 11 statistical package (Ryan & Joiner, 1994). As well as determination of statistical significance which was taken when $P_{slope} < .05$, the

importance of the slope of the regression equation was assessed from the γ_m criterion which requires that the F ratio must exceed a minimum value which we calculated for our degrees of freedom to be 25.0 (Draper & Smith, 1981). Other comparisons viz. between leftwards and rightwards saccadic latencies, between overlap and gap paradigms, and between different runs were made by analysis of variance (ANOVA) when statistical significance was again taken as $P < .05$.

3. Results

Three experiments were undertaken each with four subjects.

3.1. Experiment 1

In this experiment, saccadic latencies were obtained for leftwards and rightwards presentation of the target in random order for overlap and gap paradigms over a range of 5–35° in 2 runs. There was no significant difference between latencies for the left or rightwards saccades ($P = .06$, ANOVA) and so these were pooled. There was also little evidence of a training effect. Saccadic latencies with the overlap paradigm in all four subjects and with the gap paradigm in two subjects were not significantly different between runs 1 and 2 ($P > .05$) while in two subjects there was a significant shortening of the mean latency with the gap paradigm in the second run but only by 11 and 15 ms ($P < .05$). The results for runs 1 and 2 were thus also combined.

Setting aside for the moment the differences in experimental conditions which were employed, the aggregated histograms of latencies for the four subjects showed a clear distinction between the distributions for overlap and gap paradigms (Figs. 1A and B). In the former, there is essentially a unimodal distribution with a mean latency of 223 ms which corresponds to slow regular saccades while Fig. 1B shows a distribution with an appreciably shorter peak latency of 155 ms which corresponds to fast regular saccades (Gezeck et al., 1997). There was also evidence of a second distribution with a small peak at 105 ms which was taken to consist of express saccades. To separate these from fast regular saccades, we adopted an upper cut-off of 120 ms (Gezeck et al., 1997) which fitted well with the distributions shown in Figs. 1B and D. The express saccades present in Fig. 1B were generated mainly by two subjects who had 19 and 30% latencies of less than 120 ms while, for the remaining two subjects, the percentages were only 5 and 7%.

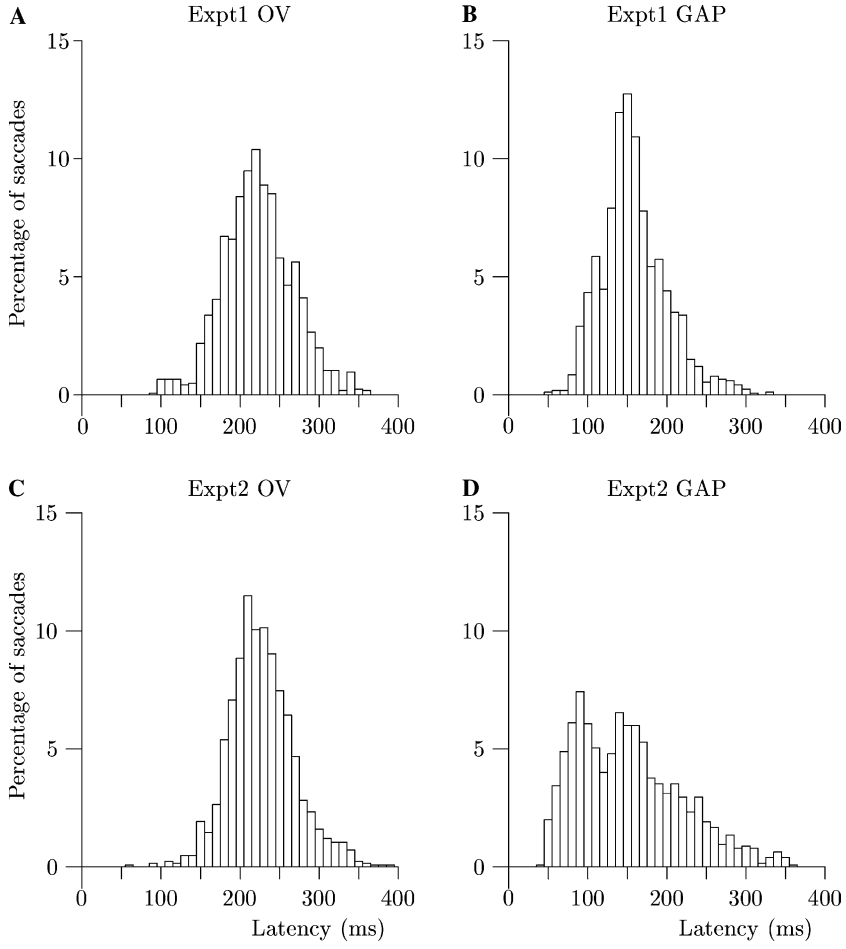

Fig. 1. Distribution of saccadic latencies expressed as a percentage of the total for the combined results of the four subjects. Experiment 1 involved left or right target presentation, Experiment 2 involved right presentation, OV is overlap paradigm and GAP is gap paradigm. Total number of saccades are A: 1655, B: 1656, C:1243, and D: 1251.

Hence, express saccades were generated relatively infrequently while the majority would qualify as fast regular saccades. With the overlap paradigm, express saccades were essentially absent (Fig. 1A).

Next, the dependence of saccadic latency on target angular displacement was examined. With the overlap paradigm, in three out of four subjects, there was a direct relationship between latency and target angular displacement which was both significant and important ($R^2 = 8$–17%, $P < .001$, $F > 32$) (Fig. 2A) while in the fourth subject, there was no relationship ($R^2 = .1\%$, $P = .45$). The results for the gap paradigm were divided into fast regular and express saccades. In the case of the former, two subjects showed an absence of a relationship ($R^2 = 1\%$, $P > .05$) (Fig. 2C) while two subjects showed a significant relationship ($R^2 = 3.7$ and 6.9%, $P < .05$) which was of doubtful importance since $F < 25$. Of the two subjects with an appreciable number of express saccades, there was an absence of a relationship between

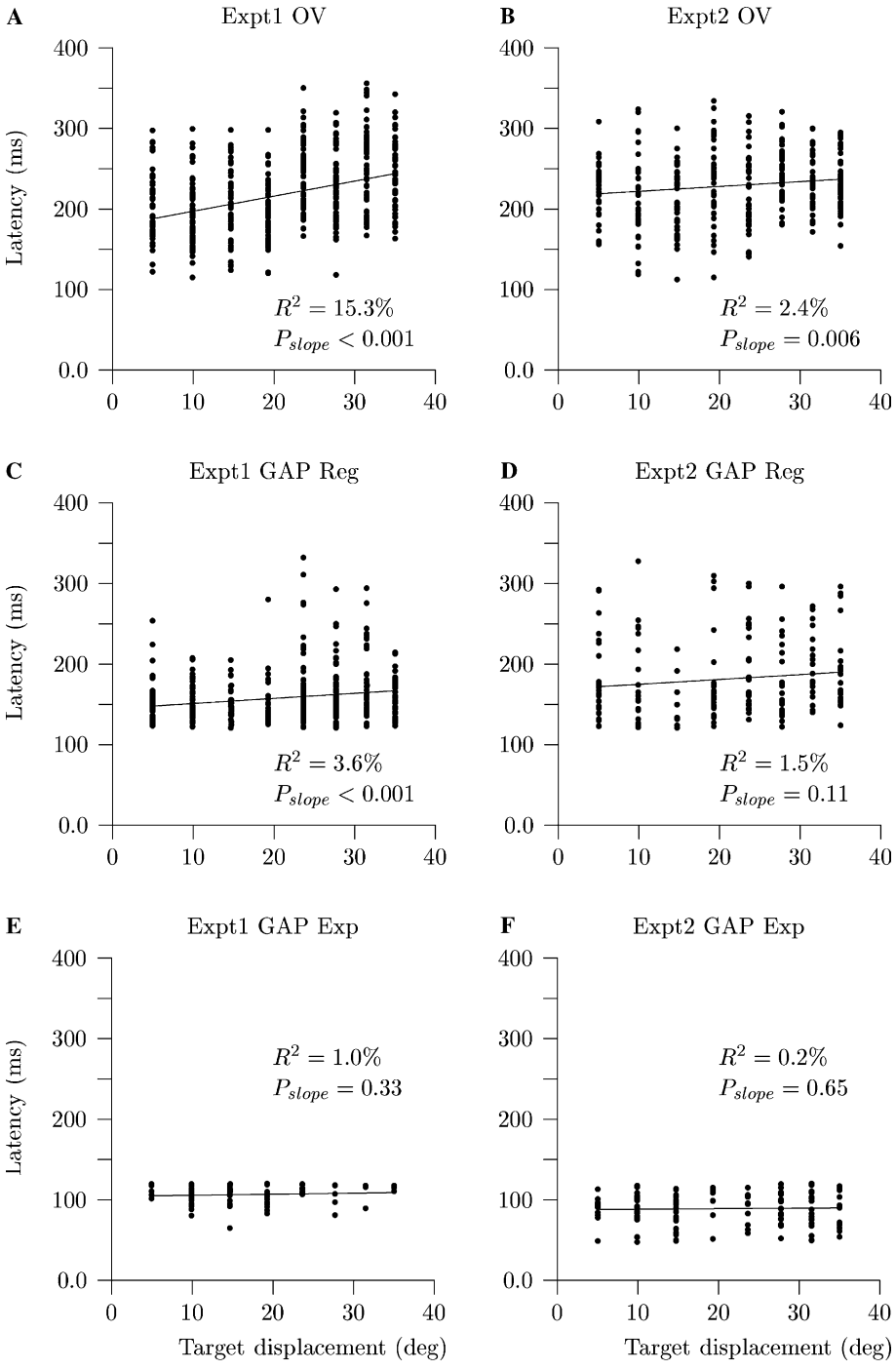

Fig. 2. Saccadic latency against target angular displacement showing best fitting regression lines. Experiment1 involved left or right target presentation, Experiment2 involved right only presentation, OV is overlap paradigm, GAP is gap paradigm, Reg indicates fast regular saccades, and Exp indicates express saccades.

latency and target angular displacement in both cases ($R^2 = 1\%$, $P = .33$)(Fig. 2E). Hence, in summary, slow regular saccades generated in response to the overlap paradigm showed increasing latency with increasing target angular displacement while fast regular and express saccades generated in response to the gap paradigm showed essentially constant latency.

3.2. Experiment 2

In this experiment, the element of uncertainty was removed by arranging for the target light spot to appear to the right of the fixation light spot. The same range of target angular displacements was used and the experimental runs were repeated three times. The mean value for the slow regular saccades was essentially unchanged at 228 ms (Fig. 1C) while there was a very marked increase in the proportion of express saccades with the gap paradigm (Fig. 1D). On a subject by subject basis, these increased from 5 to 44%, 7 to 24%, 19 to 43%, and 30 to 36% ($P < .05$, paired t test). Within the 3 runs, there was no systematic change in the proportion of express saccades in the four subjects ($P > .05$, ANOVA).

There was also a change in relationship between saccadic latency and target angular displacement with the overlap paradigm in that there was a marked reduction in the R^2 values which now ranged from 0.5 to 7% (Fig. 2B). While statistical significance was attained in three out of four subjects, the small F values of 8–23 indicate a lack of importance of these R^2 values. Fast regular saccades also showed low R^2 values of 0.4 to 6.9% with F values of less than 25 (Fig. 2D). Likewise, express saccades which were generated by all four subjects showed an absence of a relationship ($R^2 < 4.8\%$, $P > .05$) (Fig. 2F).

3.3. Control experiments on viewing distance

Since a viewing distance of 28.5 cm had been employed in order to obtain a sufficiently wide display subtense, there was the possibility that the large amount of convergence exerted might have affected saccadic latencies. We compared saccadic latencies for natural viewing at 57 cm, additional viewing through a 10 Δ prism placed base-out to induce adduction and simulate viewing at 30 cm and base-in in order to induce abduction to simulate viewing at 400 cm. The prisms were applied to each eyes in turn and the results showed that there was no effect on saccadic latencies ($P = .09$, ANOVA). This indicates that varying magnitudes of convergence were without effect on saccadic latency.

4. Discussion

Our study has produced two clear outcomes. First, the frequency of occurrence of express saccades was increased on removal of the uncertainty as to which hemifield was to contain the target light spot and, second, the latency of express saccades as well as that of fast regular and slow regular saccades remained invariant of target angular displacement when the target light spot appeared in the same hemifield.

4.1. Effects of target hemifield

With randomized leftwards or rightwards target presentation, relatively few express saccades were generated in our experiments. In these experiments, there were no asymmetries between the latencies for the two target directions which is in agreement with Baloh and Honrubia (1976), Fischer and Ramsperger (1984), and Fischer and Weber (1997) though not with Pirozzolo and Rayner (1980) and Hutton and Palet (1986) who showed shorter latencies for rightwards saccades in right handed subjects. While shortening the saccadic latency with the gap paradigm (Saslow, 1967) has been confirmed by numerous investigators, there is less agreement over the generation of express saccades. There are numerous reports of either the generation of mainly fast regular saccades of peak latency 130–180 ms (Kingstone & Klein, 1993; Reuter-Lorenz, Oonk, Barnes, & Hughes, 1995; Shafiq, Stuart, Sandbach, Maruff, & Currie, 1998; Tanaka, Yoshida, & Fukushima, 1996) or the absence of a separate population of express saccades (Pratt, 1998; Wenban-Smith & Findlay, 1991). The common feature in these studies has been the use of randomized left or right target presentation. When express saccades were reported in response to randomized target presentation, the subjects had either undergone prior training with the purpose of enhancing express saccade generation or were experienced in the experimental methods (Braun & Breitmeyer, 1988; Fischer & Weber, 1992, 1997, 1998; Kurata & Alzawa, 2004; Weber, Dürr, & Fischer, 1998; Weber & Fischer, 1994, 1995). In studies in which subjects were explicitly stated to be naive, randomized target presentation was shown to evoke express saccades in a limited proportion of subjects (Fischer et al., 1993), while non-randomized target presentation evoked far more express saccades, though this was associated with numerous anticipatory saccades which were rarely generated in the present study (Fischer & Ramsperger, 1986). The present study has combined both modes of target presentation to show that express saccade generation is markedly enhanced with non-randomized target presentation in naive subjects. However, it might be reasonably objected that, after Experiment 1, our subjects were no longer naive and this accounted for the increased frequency of express saccades in Experiment 2, though this is unlikely for two reasons. First, the duration of the training period must extend over many days (Fischer & Ramsperger, 1986) and, second, one of our subjects who undertook a trial run of the experimental protocol did not show any increase in the proportion of express saccade in Experiment 1. Express saccade generation has also been reported to depend on whether the preceding eye movement was in the same direction as the prospective saccade (Carpenter, 2001), which was not the case in the present study when the saccades in Experiment 2 were always preceded by a return eye

movement in the opposite direction. Kurata and Alzawa (2004) also failed to confirm Carpenter's result. Given that our inter-stimulus intervals were much longer than those used by Carpenter, any facilitatory effect of the preceding saccade would most likely have decayed since, for example, facilitatory effects of attentional cues are known to be effective for only several hundreds of milliseconds (Braun & Breitmeyer, 1988; Fischer & Weber, 1998).

4.2. Effects of target angular displacement

The main purpose of our study was to determine whether express saccadic latency changed with target angular displacement. In general, the studies cited in this manuscript, with the exception of that of Munoz and Corneil (1995), used only one or two small target subtenses, often 4°. In our previous study of slow regular saccades, we demonstrated the invariance of saccadic latencies with target angular displacement (Darrien et al., 2001) but had difficulty in reconciling the results with those of previous studies which showed an increase in latency (Fuller, 1996; Kalesnykas & Hallet, 1994; Shafiq et al., 1998; White, Eason, & Bartlett, 1962; Zambarbieri, Beltrami, & Versino, 1995). This issue may now be resolved since when we used targets randomized to appear to the left or right, as in the above studies, saccadic latency increased with target angular displacement (Fig. 2A). When we reverted to target presentation in the same hemifield, the results showed the same invariance of saccadic latency as before (Fig. 2B). Hence, the introduction of uncertainty as to which hemifield will contain the target has the consequence of causing saccadic latencies to increase with target angular displacement. By contrast, the result for saccades generated with the gap paradigm is different in that, even with the randomized protocol of Experiment 1, fast regular saccades and the small number of express saccades showed constant latency with target angular displacement (Figs. 2C and E). This was confirmed to be the case in Experiment 2 in which a much higher proportion of express saccades was generated (Figs. 2D and F). This expands on the reports that express saccadic latencies were unchanged on increasing the target subtense from 4° to 8° (Fischer & Ramsperger, 1986) or decreased slightly on increasing the target subtense from 1° to 12° (Fischer & Weber, 1997). So, even with the increased retinal pathlength for stimulation at 35° compared with 5°, which might be expected to add some 20 ms to the latency if conduction were assumed to be entirely by small diameter axons (Ogden & Miller, 1966), saccadic latencies remain constant. This can be readily accounted for by the faster conduction velocities of more peripheral ganglion cell axons (Ogden & Miller, 1966). However, when there is uncertainty about which hemifield will contain the target, slow regular saccades, but not express or fast regular saccades, show an additional delay which increases as eccentricity increases. Since this cannot arise from an increased conduction time within the retina, it must arise centrally and must be related to the disengagement of fixation from the fixation light.

4.3. Role of attention

The generation of express saccades has been explained in terms of a three loop model in which saccade generation is driven by a hierarchy of 3 inter-connected modules denoted ATT (Attention), DEC (Decision Making), and COM (Computation of Metrics) (Fischer, Gezeck, & Huber, 1995; Fischer & Weber, 1993; Mayfrank, Mobashery, Kimmig, & Fischer, 1986). Removal of the fixation light is proposed to lead to activation of ATT (proposed to be parietal cortex) followed by activation of DEC (proposed to be the frontal eye fields and basal ganglia). This prior excitation facilitates the effects of the visual stimulus which activates COM (proposed to be visual cortex and superior colliculus) resulting in the generation of an express saccade. The saccadic latency increases markedly if attention has to be disengaged from the fixation light as in the overlap paradigm or when an additional process is implemented as in the generation of anti-saccades in the direction opposite to the target (Fischer & Weber, 1992) or, in the case of the present study, if there is uncertainty as to which hemifield will contain the visual target.

Posner (1980) has proposed that for a saccade to be generated, attention must first be directed away from the fixation point to the target to which the saccade is to be made. Therefore, use of a gap paradigm causes a release of attention from the fixation light resulting in shorter latency saccades (Fischer & Weber, 1993). The presentation of a cue in the region of where the target is due to appear is well established as causing a shortening of saccadic latency whether the cue is visual (Fischer & Weber, 1998; Kurata & Alzawa, 2004; Madelain, Krauzlis, & Wallman, 2005), auditory (Munoz & Corneil, 1995; Reuter-Lorenz et al., 1995) or somatosensory (Amlôt, Walker, Driver, & Spence, 2003). However, by contrast, a maintained visual cue which competes for attention impairs express saccade generation (Braun & Breitmeyer, 1988; Mayfrank et al., 1986), though when the distraction is extinguished prior to target presentation, this now facilitates express saccade generation. Generally, the optimal cue-target interval for these facilitatory effects is 100–200 ms. These results, however, are not directly transferrable to those of the present study which involved endogenous orienting of attention as opposed to the exogenous orienting caused by peripheral cues. This distinction has important implications for the underlying neural processes.

4.4. Neural basis of attention

There is a considerable body of evidence from both primate and human studies that the parietal cortex plays a role in the direction of attention towards exogenous cues. Neurones of the lateral intra-parietal (LIP) cortex show increased firing rates when there is an intention to make a saccade (Snyder, Batista, & Andersen, 2000). In man,

lesions of the parietal cortex impair disengagement of attention from a viewed object (Posner, Walker, Friedrich, & Rafal, 1984) while positron emission tomographic (PET) studies show activation of the superior parietal cortex on attention shifts to the peripheral visual field (Corbetta, Miezin, Shulman, & Petersen, 1993). The results for sustained shifts of attention to either of the visual hemifields, however, showed activation of ventral extra-striate cortex without activation of parietal cortex (Heinze et al., 1994). This may be related to the neuronal activity of areas V2 and V4 which is enhanced when attention is directed towards the receptive field of the neurone (Luck, Chelazzi, Hillyard, & Desimone, 1997). This is also consistent with the augmentation of the P1 component of the event-related potential recorded from human subjects when attention was directed towards one side of the display (Heinze, Luck, Mangun, & Hillyard, 1990). Unlike parietal neurones which have very large receptive fields which span the vertical meridian (Gnadt & Anderson, 1988), the neurones of prestriate areas V2 and V4 have small receptive fields restricted to within one visual hemifield (Luck et al., 1997) which means that integration between hemifields must involve callosal transfer of information. This may be a factor in causing an extended saccadic latency when there is uncertainty about which hemifield will contain the visual target and hence in precluding express saccade generation.

5. Conclusions

With randomized leftwards or rightwards target presentation, there was infrequent generation of express saccade in response to the gap paradigm while slow regular saccades evoked by the overlap paradigm showed an increasing delay in the latency with increasing target angular displacement. By contrast, non-randomized target presentation to the same hemifield led to much more frequent express saccade generation and constant saccadic latency for slow regular, fast regular, and express saccades with increasing target angular displacement. Under these circumstances, it is concluded that saccade generation system operates at the shortest latency irrespective of the target eccentricity.

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